

Geographic distribution and conservation of *Bothriechis aurifer* (Salvin, 1860) (Squamata, Viperidae)

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Abstract. The known distribution of *Bothriechis aurifer* (Salvin, 1860) is outdated, which impedes an accurate evaluation of its conservation status. Here, we clarify the locality-level distribution of *B. aurifer* and announce a 101-km range extension. Based on this and other data, we recommend its recategorization as Endangered under the International Union for Conservation of Nature's Red List of Threatened Species, and its addition to Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora. We also discuss problematic previous records and offer conservation recommendations. A complete Spanish translation of this paper is available in the Supplemental Data. Una traducción completa al español de este artículo está disponible en los Datos Suplementarios.

Key words. Altiplanicie de Chiapas, Central Plateau, Guatemala, Mesoamerica, Mexico, endangered species, venom

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INTRODUCTION

Accurate and detailed geographic distribution maps are fundamental for documenting biological diversity (Ficetola et al. 2014; Nogueira et al. 2019). Such maps are also crucial for guiding actions aimed at protecting endangered species (Guisan et al. 2013; Palacio et al. 2021; Serrano et al. 2023). Unfortunately, knowledge of species distributions is often incomplete (Hortal et al. 2015). Distribution data is especially scarce for many snake species, largely due to their rarity and secretive habits that make them difficult to observe (Durso et al. 2011; Nogueira et al. 2019; Serrano et al. 2023).

Among the reptile diversity of tropical America, snakes of the genus *Bothriechis* Peters, 1859 have long intrigued researchers and hobbyists because of these snakes' rarity, venom, and striking coloration (Campbell and Lamar 2004; Luna-Reyes and Suárez-Velázquez 2008; Meléndez 2008). Members of the genus are semi-arboreal, with adaptations for this microhabitat that include a prehensile tail and usually green coloration (Campbell and Lamar 2004). *Bothriechis* species generally inhabit humid mountain forests, and they are distributed from the Isthmus of Tehuantepec in southern Mexico to northwestern Peru and eastern Colombia (Arteaga et al. 2024). Four species of *Bothriechis* are found in Mexico: *B. aurifer* (Salvin, 1860) and *B. bicolor* (Bocourt, 1868) in the state of Chiapas, and *B. nigroadspersus* (Steindachner, 1870) plus *B. rowleyi* (Bogert, 1968) in Chiapas and Oaxaca (Jiménez-Lang et al. 2002; Campbell and Lamar 2004; Wylie & Grünwald 2016; Clause et al. 2020; Arteaga et al. 2024). Because of their furtive habits and cryptic coloration, most species of this genus are poorly studied, poorly sampled, and poorly represented in Mexican museum collections (Bogert 1968; Smith and Moll 1969; Mason et al. 2019).

One of the rarest species of the genus is *Bothriechis aurifer* (Salvin, 1860), Yellow-blotched Palm-pitviper. This species is known from the Sierra de Las Minas in Guatemala westward to extreme southern Mexico, in mountainous areas from 1200–2300 m elevation (Campbell and Lamar 2004; Köhler 2008). The venom



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of *B. aurifer* is sufficiently potent to have caused several deaths in Guatemala (Campbell and Lamar 2004), and hence knowledge of its geographic distribution has implications for public health. The species is imperiled range-wide, due primarily to the destruction, fragmentation, and disturbance of its habitat, but also due to illegal trafficking for the pet trade (Meléndez 2008; Campbell and Muñoz-Alonso 2014; Auliya et al. 2016; Hidalgo-García et al. 2018). Based in part on these factors, *B. aurifer* is categorized as “Amenazada” [Threatened] in the NOM-059-SEMARNAT-2010 list of the Mexican federal government, and as “Vulnerable” in the Red List of Threatened Species of the International Union for Conservation of Nature.

Despite its high profile and relevance to human health, scientific knowledge of *B. aurifer* remains surprisingly sparse and outdated. The three most recent locality-level distribution maps for the species differ greatly in the number of localities presented (5, 10 and 21 localities; Köhler 2008, Campbell and Lamar 2004, and Hidalgo-García et al. 2018, respectively), and these authors provide minimal supporting evidence to verify these localities. Furthermore, although known for more than 80 years, the presence of *B. aurifer* in Mexico remains imprecise in many aspects. Martín del Campo (1938, 1950) was the first to report *B. aurifer* from Chiapas, but it is impossible to identify exactly where he found the species (Casas-Andreu and Smith 1990; Campbell and Frost 1993; Peterson and Nieto-Montes de Oca 1996). Subsequently, Miguel Álvarez del Toro (1973, 1982) reported the presence of *B. aurifer* in Chiapas using only ambiguous language such as “Selvas cerca de los ríos Usumacinta y Lacantum” [Forests near the Usumacinta and Lacantum = Lacantún rivers]. More recently, Heimes (2016) and Hidalgo-García et al. (2018) reported the species from several localities in Chiapas, but they provided few details about these findings. Without a current and well-supported understanding of the geographic distribution of *B. aurifer* in both Mexico and Guatemala, no accurate assessment can be made of its conservation status, which was last analyzed a decade ago (Campbell and Muñoz-Alonso 2014).

The objective of this study is to update the known geographic distribution of *B. aurifer*, using data from our recent fieldwork in Mexico together with a comprehensive review of museum specimens, scientific literature, and citizen science platforms. Based on this review, we extend the species’ known range, discuss problematic Mexican records, propose changes to the species’ inclusion in two international lists of threatened species, and offer recommendations for its protection.

METHODS

To comprehensively evaluate the geographic distribution of *Bothriechis aurifer*, we consulted multiple sources of information. First, we gathered data on specimens preserved in museum collections by cross-referencing data from the Global Biodiversity Information Facility (GBIF) (<https://doi.org/10.15468/dl.4t9gfv>), VertNet (<https://vertnet.org/>), and the scientific literature using the Web of Science (<https://www.webofscience.com>) and Scopus (<https://www.scopus.com>) with “*Bothriechis aurifer*” as search keywords. To resolve inconsistencies, obtain more detailed information, or discover specimens from collections that are unpublished in GBIF and VertNet, we requested and reviewed data from the following collections: American Museum of Natural History (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); California Academy of Sciences (CAS); Colección Nacional de Anfibios y Reptiles (CNAR); El Colegio de la Frontera Sur, Unidad Chetumal (ECO-CH-H); El Colegio de la Frontera Sur, Unidad San Cristóbal de las Casas (ECO-SC-H); Colección Zoológica Regional Herpetológica de la Secretaría de Medio Ambiente e Historia Natural (CZR-HE); Colección Herpetológica del Museo de Zoología “Alfonso L. Herrera” de la Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC-HE); Florida Museum of Natural History (UF); Field Museum of Natural History (FMNH); Natural History Museum of Los Angeles County (LACM); Smithsonian Institution National Museum of Natural History (USNM); University of Michigan Museum of Zoology (UMMZ); University of Texas at Arlington (UTA); and Museo de Zoología de la Universidad de Ciencias y Artes de Chiapas (MZ-UNICACH). The taxonomic identity of the museum specimens was verified by collections staff, and we personally reviewed the specimens deposited in the ECO-SC-H, ECO-CH-H, CZR-HE, and MZ-UNICACH collections. Additionally, we directly contacted observers of biogeographically relevant records on iNaturalist (<https://www.inaturalist.org>) to obtain precise coordinates, because this platform obscures precise location data for many species including *B. aurifer* (see Contreras-Díaz et al. 2023).

We complemented this review with our own records based on recent fieldwork in Chiapas, Mexico. Some of these field records were mentioned previously (Hidalgo-García et al. 2018), but detailed information for each is provided herein for the first time. For each observation, we deposited a photographic record either in the Digital Collection of the University of Texas at Arlington (UTADC) or in the photographic collection of the Department of Herpetology of the Natural History Museum of Los Angeles County (LACM PC). In one case, we instead collected (scientific collection permit SGPA/DGVS 01609/16) a tissue sample in 95% ethanol and then fixed the rest of the snake’s body in 10% formalin and preserved it in 70% ethanol prior to deposition in the ECO-CH-H. For color descriptions, we consulted the guide by Köhler (2012).

To georeference historical records, we used Google Earth Pro v. 7.3.3.7786, GEOlocate v. 3.22 (Ríos and Bart 2010), and the published literature (Alcocer et al. 2016). We eliminated any literature records with contradictory elevation data and location descriptions, as well as those with incomplete, doubtful, or unverifiable information (details available in the Discussion). We considered a record to represent a locality

only when separated from all other records by at least 1 km in a straight line; if individual records were less than 1 km apart, we selected only one record from the cluster to report and map as a locality (Clause et al. 2020). We generated the distribution map with QGIS v. 3.16.3 (QGIS Development Team 2020), using WorldClim coverage (Hijmans et al. 2005) with a resolution of 0.86 km².

We reviewed the categorization of *B. aurifer* in five international and national lists of threatened species: (1) International Union for Conservation of Nature (IUCN) Red List of Threatened Species, (2) Environmental Vulnerability Score (EVS) (Johnson et al. 2015a), (3) Norma Oficial Mexicana NOM-059-SEMARNAT-2010 (SEMARNAT 2010), (4) Especies Amenazadas de Fauna Silvestre de Guatemala (CONAP 2021), and (5) Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) appendices (CITES 2019). Because *B. aurifer* is commercialized and illegally trafficked for the pet trade (Meléndez 2008; Campbell and Muñoz-Alonso 2014; Auliya et al. 2016), we rounded the GPS coordinates of the reported localities to two decimal places and provided neither distance nor direction from the nearest town. We consider these steps sufficient to balance the risks and benefits of publicly sharing geographic data for this species (Tulloch et al. 2018).

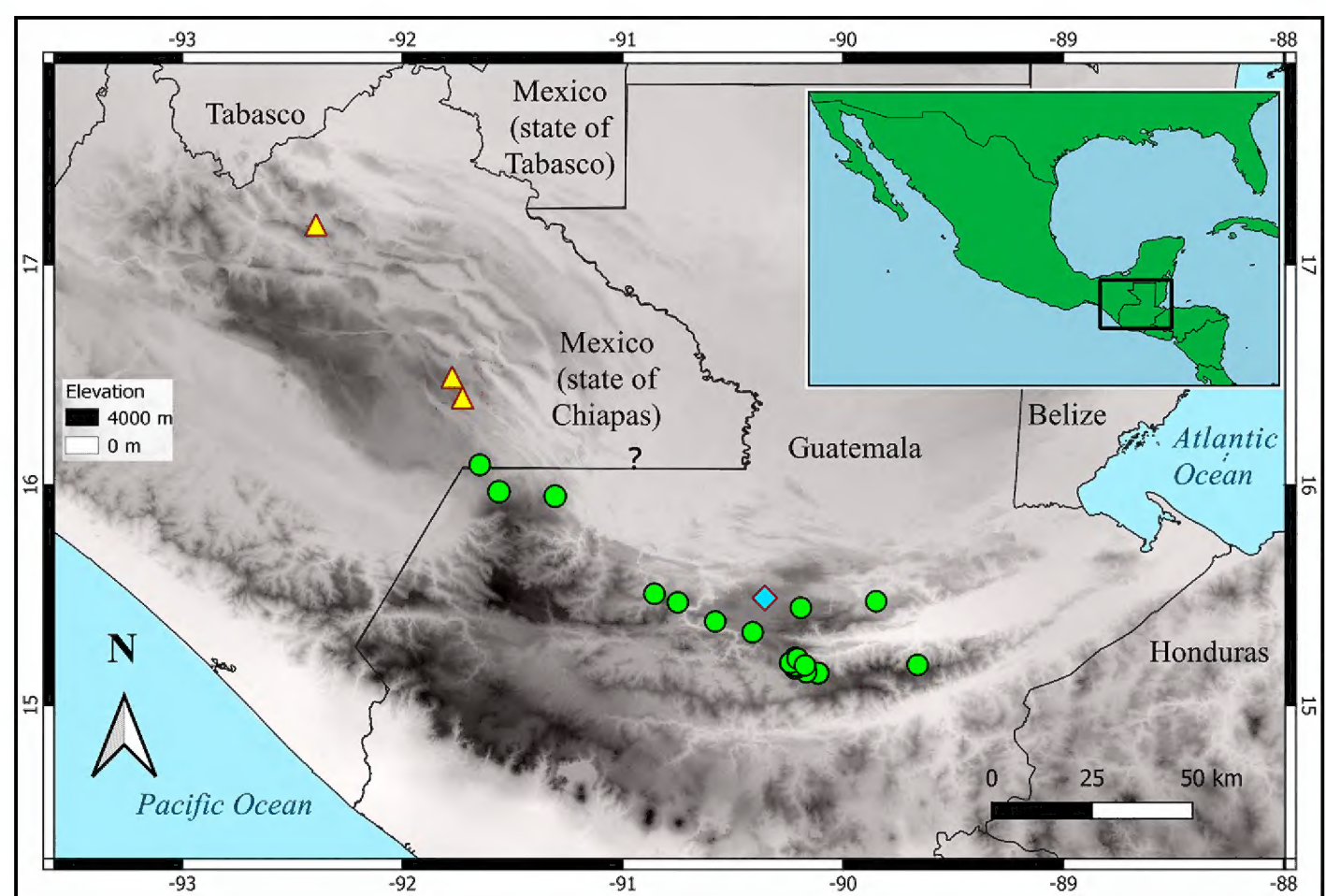
To re-evaluate the categorization of *B. aurifer* in the IUCN Red List (IUCN 2012), we calculated its area of occupancy (AOO) and extent of occurrence (EOO) as defined by the IUCN (2019). To calculate AOO, we summed all grid cells containing one or more localities across 2 × 2 km squares with the GEOCAT program (Bachman et al. 2011). To calculate EOO, we used two approaches: (1) drawing a minimum convex polygon around all verifiable and geospatially explicit localities with the program Google Earth Pro v. 7.3.3.7786, and (2) referencing the predicted distribution of *B. aurifer* as modeled by Hidalgo-García et al. (2018).

To determine if *B. aurifer* localities lie within protected areas, we superimposed the recorded localities over the boundaries of internationally recognized protected areas in Mexico and Guatemala. We downloaded the protected area boundaries (.shp files) from the World Database of Protected Areas (UNEP-WCMC and IUCN 2021).

RESULTS

We obtained 24 localities for *Bothriechis aurifer*. Of these, 20 lie in the mountains of central Guatemala and four in the mountains of southern Mexico in the state of Chiapas (Figure 1, Table A1), from ca. 1210–2260 m elevation. In Guatemala, *B. aurifer* has been recorded from five Departments: Alta Verapaz, Baja Verapaz, El Quiché, Huehuetenango, and Zacapa (Table A1). In Chiapas, *B. aurifer* has been recorded from two physiographic regions in the southern and eastern portions of the state: the Northern Highlands, and the Central Plateau, the latter is also commonly known by the alternative names Altiplanicie de Chiapas, Meseta de Chiapas, or Meseta Central. The four localities from Chiapas include six records with detailed data: one historical record from the Municipality of La Trinitaria (Álvarez del Toro 1982; GBIF 2022); two records from the Municipality of Las Margaritas (previously mentioned in Hidalgo-García et al. 2018); and three new records

Figure 1. Geographic distribution of *Bothriechis aurifer*. Yellow triangles represent records obtained during our recent fieldwork; from south to north the localities are: Felipe Carrillo Puerto, Santiago Guelatao, and El Delirio/Linda-vista Vesubio. Green circles represent other documented records. Blue diamond indicates the type locality for the species. Question mark indicates a problematic record (Chajul Biological Station) that is covered in the Discussion.



from the Municipality of Yajalón. Taken together, the Yajalón records substantiate a 101-km northwestern range extension for *B. aurifer* relative to the Las Margaritas records first announced by Hidalgo-García et al. (2018). Complete information for all records from Chiapas, Mexico is presented for the first time below. Several additional problematic Mexican records for the species are also covered in detail in the Discussion.

***Bothriechis aurifer* (Salvin, 1860)**

Figures 2A–D, 3A–D

Historical record. MEXICO – CHIAPAS • Municipality of La Trinitaria, Parque Nacional Lagunas de Montebello, between Dos Lagunas and Tzizcao [=Tziscão]; [16.09, –091.65]; 1650 m elevation; 01.XII.1979; Miguel Álvarez del Toro leg.; MAT 1148, specimen lost.

New records. MEXICO – CHIAPAS • Municipality of Las Margaritas, near Santiago Guelatao; 16.49, –091.77; 1950 m elevation; 9.X.2013, 10:30 h; Eliázar Gómez obs.; cloud forest (Figure 4A); 1 adult, sex indet., UTADC 9407, specimen photographed and not collected • Municipality of Las Margaritas, near Felipe Carrillo Puerto; 16.39, –091.73; 1660 m elevation; 26.II.2016, 10:00 h; Jorge Arturo Hidalgo-García leg.; secondary vegetation near edge of cloud forest, specimen found on branch of a shrub (“Pomac” tree) 1.5 m above ground, near a path; 1 adult, sex indet., ECO-CH-H-3770 • Municipality of Yajalón, near El Delirio; 17.18, –092.39; 1600 m elevation; 08.X.2022; 15:52 h; José García González obs.; evergreen rainforest, climbing thin trunk of a tree in the genus *Clusia*, supported by the thin fallen trunk of a fern in the genus *Campylo-neurum* 30 cm above ground, on the ridgeline of a hill; 1 adult, sex indet., LACM PC 3001, specimen photographed and not collected • Same locality as the preceding; 13.X.2022; 23:12 h; Emmanuel Javier-Vázquez, Marco A. Vázquez-Cigarroa, Gaspar Moreno, and José García González obs.; evergreen rainforest, among various species of ferns and bryophytes, primarily mosses, all wet from rain; 1 adult, sex indet., LACM PC 3002, specimen photographed and not collected • Municipality of Yajalón, near Lindavista Vesubio; 17.18, –092.39; 1540 m elevation; 01.V.2023; 00:55 h; Julio Santiago Juárez Pérez, Rigoberto Rosemberg Méndez Díaz, Jorge Arturo Hidalgo-García, José Manuel Toledo-Morales, Marcos Joaquín Fitz-Pérez, and Quetzi Tonantzin Gordillo-Pablo obs.; evergreen rainforest, specimen found on a fallen trunk 15 cm above ground, in a site with abundant leaf litter and nearby tree ferns, during a night of clear skies (10% cloud cover), 17.5 °C, 99% humidity (Figure 4B); 1 adult, sex indet., LACM PC 3005 and 3010, specimen photographed and not collected.

Identification. *Bothriechis aurifer* is distinguished from congeners by having a black postocular stripe and a green dorsum with small yellow spots bordered in black; however, some specimens have a uniform green dorsum and lack postocular stripes (Campbell and Lamar 2004). LACM PC 3001 has a chartreuse green dorsum with very diffuse dorsal spots, along with a pale cyan postocular stripe (Figure 3A). Additionally, LACM PC 3002 has pale Caribbean-blue spots with some black dots in the postocular stripe, along with

Figure 2. *Bothriechis aurifer* from the Municipality of Las Margaritas, Chiapas, Mexico. **A.** Individual from Santiago Guelatao (UTADC 9407). **B–D.** Adult from Felipe Carrillo Puerto (ECO-CH-3770). Photographs: Eliázar Gómez (A) and JRCV (B–D).





Figure 3. *Bothriechis aurifer* from the Municipality of Yajalón, Chiapas, Mexico. **A.** First adult from El Delirio (LACM PC 3001). **B.** Second adult from El Delirio (LACM PC 3002). **C, D.** Adult from Lindavista Vesubio (LACM PC 3010 and 3005). Photographs: JGG (A, B) and Quetzi Tonantzin Gordillo-Pablo (C, D).

pale Caribbean-blue color on the edges of some dorsal scales and on the tail (Figure 3B).

Other morphological details for our recent records of *B. aurifer* in Chiapas are described below. UTADC 9407: emerald-green dorsum with a thin black line along the back, black postocular stripes with yellow-green edges (Figure 2A). ECO-CH-H-3770: 3 intersupraoculars; 10 supralabials; 12 infralabials; 162 ventrals; 64 subcaudals; entire anal; lacunar scale fused with labials; snout-vent length (SVL) 602 mm; tail length (TL) 130 mm; head width (HW) 22.2 mm; weight 90 g; olive green coloration in preserved specimen (Figure 2B–D). LACM PC 3001: chartreuse green dorsum with pale lime green venter, greenish gray pupil, thin pale cyan postocular stripe (Figure 3A). LACM PC 3002: bright pale grass-green dorsum with paler venter, greenish gray pupil, pale Caribbean-blue spots on some scale edges in postocular stripe and with some black dots, lemon yellow dorsal spots with pale Caribbean-blue edges to some dorsal scales, black and yellow spots on tail faintly pigmented pale Caribbean-blue (Figure 3B). LACM PC 3005 and 3010: pale grass-green dorsum with yellow-green venter, paler yellow-green dorsal spots, black postocular stripe, gray iris with black dots or reticulations; 2 intersupraoculars; 10 supralabials; 10 infralabials; supralabial scale 2 fused with prelacunar; 16 mid-body dorsal scale rows; 155 ventrals; 58 subcaudals; entire anal; SVL 660 mm; TL 131 mm; HW 23 mm (Figure 3C, D).

Conservation status. In the Norma Oficial Mexicana list (SEMARNAT 2010), *B. aurifer* is categorized as “Amenazada” [Threatened]. On the list of Especies Amenazadas de Fauna Silvestre de Guatemala (CONAP 2021), it is in Category 2 “En Peligro” [Endangered]. Johnson et al. (2015a) assigned *B. aurifer* an EVS of 15, thus placing it in the High Vulnerability category. We consider the EVS reassessment of Johnson et al. (2015a) to be the most accurate, because it considers *B. aurifer* to be a habitat specialist that is found in

Figure 4. Habitat of *Bothriechis aurifer* in Chiapas, Mexico. **A.** Cloud forest near Santiago Guelatao, where individual UTADC 9407 was found. **B.** Evergreen rainforest near Lindavista Vesubio, where individual LACM PC 3005 and 3010 was found. Photographs: JAHG (A) and Quetzi Tonantzin Gordillo-Pablo (B).



fewer vegetation types (5 versus 6) compared to previous evaluations (Wilson et al. 2013; Johnson et al. 2015b). We recommend no changes to the SEMARNAT, CONAP, or EVS categorizations. On the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN), *B. aurifer* is categorized as “Vulnerable” (Campbell and Muñoz-Alonso 2014). Using the minimum convex polygon, we estimated an EOO of 15,691 km². However, due to the topography of the mountains that support *B. aurifer* (Figure 1), this is an overestimation that includes extensive areas of lowlands inappropriate for the species. Using the potential distribution model published by Hidalgo-García et al. (2018), the EOO of *B. aurifer* is 5,254 km², and we consider this to be the more appropriate EOO value. Both values are within the upper limit for categorization as “Vulnerable” (EOO < 20,000 km²) on the IUCN Red List (IUCN 2019). Finally, we calculated an AOO of 92 km² for the species, which is within the upper limit for categorization as Endangered (AOO < 500 km²) (IUCN 2019). Based in part on this AOO estimate, we recommend that *B. aurifer* be re-categorized as Endangered (criterion B2ab[iii]) on the IUCN Red List. Additionally, *B. aurifer* is not listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) appendices (CITES 2019), yet because illegal trafficking is documented (Campbell and Muñoz-Alonso 2014; Auliya et al. 2016), we recommend that the species be added to Appendix I of CITES. We present further justification for these two proposed changes in the Discussion.

Records of *B. aurifer* occur in seven protected areas in Guatemala, and one in Mexico. Throughout its distribution (Guatemala and Mexico), only a third of the known localities of *B. aurifer* are located within a protected area, including only one (25%) of the four verified localities in Mexico.

DISCUSSION

There is little clarity regarding historical records of *Bothriechis aurifer* in Mexico. For over half a century, many authors have identified *B. aurifer* as being distributed in Chiapas, Mexico (Martín del Campo 1950; Campbell and Lamar 1989; Campbell and Lamar 2004; Köhler 2008; Luna-Reyes and Suárez-Velázquez 2008; Campbell and Muñoz-Alonso 2014; Johnson et al. 2015b; Heimes 2016). But prior to the localities announced by Hidalgo-García et al. (2018), all published literature reporting this species in Chiapas referenced only vague and/or unverifiable records. We therefore excluded those problematic localities from our results, because none of them could be accurately mapped. However, for transparency we briefly discuss these records below in chronological order.

The first report on the existence of *B. aurifer* in Mexico involved a Chiapas specimen collected by Mario del Toro Avilés, supposedly between June and August 1937 from “Santa Rosa, de la region de Comitán, cercana a Guatemala” [Santa Rosa, in the Comitán region, near Guatemala] (Martín del Campo 1938). A black and white photograph and a brief description of the preserved color of this specimen are available (Martín del Campo 1938), and both are consistent with *B. aurifer*. The identity of this specimen, which was originally called *Bothrops nigroviridis aurifera* (a synonym of *Bothriechis aurifer*), has never been questioned in the literature. However, this specimen, which according to Martín del Campo (1938) was donated to the “Instituto de Biología” collection of the Universidad Nacional Autónoma de México, is now lost; we requested information from the database of this collection (now known by the acronym CNAR; Sabaj 2020), but no records of *B. aurifer* were found. More importantly, there is great confusion regarding the geographic location of this record. Seven towns named Santa Rosa exist within 35 km of the city of Comitán de Domínguez, Chiapas (CEIEG 2021), and none of these towns are within the modeled distribution of this species (Hidalgo-García et al. 2018). Other authors have concluded that the locality and/or date information linked to additional vertebrate specimens supposedly collected by Mario del Toro Avilés on his expedition to “Santa Rosa” is unreliable (Casas-Andreu and Smith 1990; Campbell and Frost 1993; Peterson and Nieto-Montes de Oca 1996). We support that conclusion. Pending the formal publication of new and detailed data, the presence of *B. aurifer* in the Comitán region should, at best, be considered questionable.

Some 50 years later, in the third edition of his book *Los Reptiles de Chiapas*, Miguel Álvarez del Toro (1982) mentioned the presence of *B. aurifer* in the southeastern Chiapas Highlands and nearby areas. Using the synonym *Bothrops nigroviridis*, Álvarez del Toro (1982: 212) indicated that the species “Vive en las selvas que cubren los pequeños cerros de la parte oriental de la llamada Selva Lacandona, especialmente hacia las alturas que se encuentran con rumbo a la frontera con Guatemala, ya aproximándose al Municipio de Comitán, pero sin llegar a los climas templados” [Lives in the forests that cover the small hills in the western part of the so-called Selva Lacandona, especially towards the highlands that are found near the Guatemala border, approaching the Municipality of Comitán, but without reaching the temperate climates]. The book also contains a color photograph titled “Nauyaca manchada (*Bothrops aurifer*)” (Figure 166). A different color photograph taken by Álvarez del Toro of this same specimen, which clearly represents *Bothriechis aurifer*, is provided by Luna-Reyes and Suárez-Velázquez (2008: 42). In his concluding list of species, Álvarez del Toro (1982: 232) provides more information as follows: “*Bothrops nigroviridis* (Salvin) Nauyaca Verdinegra. Selvas cerca de los ríos Usumacinta y Lacantum” [*Bothrops nigroviridis* (Salvin) Nauyaca Verdinegra. Forests near the rivers Usumacinta y Lacantum = Lacantún] and “Nauyaca Manchada *Bothrops aurifer*. Se encuentra en los cerros al oriente de Comitán, en los lugares de vegetación selvática” [Nauyaca

Manchada *Bothrops aurifer*. It is found in the hills east of Comitán, in places with jungle vegetation]. Although the exact provenance of the *B. aurifer* specimen in the photographs is unknown, it seems evident that Álvarez del Toro was personally familiar with the species. Therefore, although lacking an unequivocal link between these photographs and the now-lost specimen collected by Álvarez del Toro in 1979 (MAT 1148), we consider the locality of said specimen to be valid (Figure 1, Table A1).

Almost 40 years after Álvarez del Toro's record, Heimes (2016) indicated that *B. aurifer* "is known from the areas of Lagos de Montebello and Montes Azules," and included two color photographs of *B. aurifer* (figures 483 and 484) taken by Antonio Ramírez Velázquez from "ANP Lagos de Montebello, municipio de la Trinitaria, Chiapas." ANP is undoubtedly an acronym for Área Natural Protegida [Protected Natural Area], so the locality description represents an alternative name for the Lagunas de Montebello National Park. Because the area of overlap between this park and the Municipality of La Trinitaria exceeds 5,000 ha, we were unable to map this record as a different locality from the lost specimen (MAT 1148). Therefore, we excluded the Heimes (2016) record from our results.

Additionally, the Global Biodiversity Information Facility (GBIF, <https://doi.org/10.15468/dl.4t9gfv>) contains two other problematic records of *B. aurifer* from Chiapas. The first corresponds to a locality called Paraje Yashanal, Municipality of Tenejapa, for which no supporting evidence is available. Although potential distribution models predict that this locality is suitable for the species (Hidalgo-García et al. 2018), we consider this record to necessitate confirmation with photographic or physical evidence. The second record is from the Chajul Biological Station, Municipality of Ocosingo, which is based on a specimen from the collection of the Museo de Zoología "Alfonso L. Herrera" of the Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC-HE 7596). Upon review, we concluded that this juvenile specimen is correctly identified because it: (1) has very large scales on the top of the head, between and in front of the eyes; (2) has several large, pale vertebral spots wholly or partially surrounded by dark pigment; and (3) lacks a pronounced, upturned snout. However, it was recorded in an area outside the modeled distribution for *B. aurifer* (Hidalgo-García et al. 2018). The elevation and type of habitat (160 m, tropical forest) of the Chajul Biological Station are also unlike any other confirmed locality for the species. We therefore conclude that the locality data is probably erroneous. This presumed locality could also explain why Heimes (2016) indicated that *B. aurifer* is found in Montes Azules, because the Chajul Biological Station lies within the boundaries of the Montes Azules Biosphere Reserve.

Because two of the three historical specimens of *B. aurifer* from Mexico mentioned above (that of Martín del Campo [1938] and that of Álvarez del Toro [1982]) are lost, and because the third specimen (MZFC-HE 7596) is of dubious origin, the only reliable Mexican specimen for the species deposited in a scientific collection is ECO-CH-3770. This record from Felipe Carrillo Puerto, Municipality of Las Margaritas, Chiapas (Figure 2B–D), plus an individual of *B. aurifer* that was photographed in Santiago Guelatao in the same municipality (UTADC 9407; Figure 2A) were first mentioned by Hidalgo-García et al. (2018), but herein we provide supporting details for the first time. The three new records from El Delirio/Lindavista Vesubio in the Municipality of Yajalón, Chiapas that we announce here constitute the northwestern-most records for *B. aurifer*, and the first for the Northern Highlands physiographic region of Chiapas. These three records extend the known distribution for the species 101 km northwest of the nearest previous record from Santiago Guelatao (Hidalgo-García et al. 2018), and 145 km northwest of the historical record (MAT 1148) from the Lagunas de Montebello National Park.

This northwestern range extension of *B. aurifer* reduces the distance between the species and its congener *B. rowleyi* in the Northern Highlands. Less than 60 airline km separate El Delirio/Lindavista Vesubio from the easternmost record of *B. rowleyi* at 22.2 km south of Tapilula on Highway 195 (Campbell and Lamar 1989; Gutberlet 1995; Grünwald et al. 2016). In this region, the lowland canyons of the Río Tacotalpa and Río Chacté divide the high mountains to the west and east. These river valleys could serve as a biogeographic barrier isolating *B. aurifer* from *B. rowleyi*, which are sister species that diverged approximately 7–9 million years ago (Mason et al. 2019). We hope that future fieldwork in the Northern Highlands and Central Plateau physiographic regions will lead to further advances in biogeographic knowledge of *Bothriechis*. We echo other authors in arguing for greater investment in such fieldwork efforts (Hortal et al. 2015; Wilson 2017). Verifying the continued presence of *B. aurifer* within the Lagunas de Montebello National Park is especially needed, because it is the only Mexican protected area known to support the species.

Regarding the natural history of *B. aurifer*, during our fieldwork we documented two specimens active at night on different dates (11:12 h on 13.X.2022 and 00:55 h on 01.V.2023) in the Municipality of Yajalón. Such nocturnal activity has rarely been recorded for this species (Arrivillaga et al. 2018); it was previously thought to be strictly diurnal (Campbell and Lamar 2004).

There are three main threats to the survival of *B. aurifer*, which provide important justification for our proposed re-categorizations on the IUCN Red List and CITES appendices. The most important threat is the destruction and fragmentation of the species' cloud-forest habitat. The extensive conversion of these forests to agricultural fields has been documented for decades, and it is happening throughout the species' range in both Guatemala and Mexico (Campbell and Lamar 2004; Cortina-Villar et al. 2004; Campbell and Muñoz-Alonso 2014; Pope et al. 2015; Hidalgo-García et al. 2018; Elsen et al. 2020). For example, in and near the same mountain range as our recent records of *B. aurifer* from Las Margaritas, Chiapas, JAHG

has observed extensive deforestation. Through conversations with residents, we confirmed that in some localities the cloud forest there is being cut down to make way for pine (*Pinus* sp.) plantations, which the landowners or ejidatarios sell to sawmills or other consumers in the Central Plateau physiographic region. Another threat to the habitat of *B. aurifer* is climate change. Cloud forest is an ecosystem that is particularly vulnerable to this phenomenon (Elsen et al. 2020). According to climate models, the area of cloud forest is estimated to suffer a reduction of 87% in Chiapas by the year 2080 (Ponce-Reyes et al. 2012), and a reduction of 54–76% in Mexico by the year 2050 (Rojas-Soto et al. 2012). In addition to habitat loss from deforestation and climate change, a secondary threat to *B. aurifer* is illegal harvesting for the national and international hobbyist black market (Auliya et al. 2016; Campbell and Muñoz-Alonso 2014). There is also unpublished information that *B. aurifer* is being illegally trafficked in Chiapas, probably for sale in the pet trade (Víctor Moreno Avendaño and Otoniel Jiménez Lang pers. comm.).

Based on this information regarding threats, there is strong support for an inference of continued decline in the area, extent, and quality of habitat for *B. aurifer*. Together with our calculated AOO value of 92 km², the species minimally meets criterion B2ab(iii) for re-categorization as Endangered on the IUCN Red List. Furthermore, although published evidence is limited due to the clandestine nature of black markets (Salzberg 1996), we consider it reasonable to conclude that wild-collected *B. aurifer* individuals are being trafficked into and out of range countries, which justifies its addition to Appendix I of CITES.

The low representation of *B. aurifer* in protected areas, particularly in Mexico, is an additional cause for concern. In the Central Plateau of Chiapas, it is necessary to establish more reserves in areas that lack protection and where at-risk species such as *B. aurifer* live. Almost all the existing protected areas in this physiographic region are small and are found only in the central part, outside the known and predicted distribution of *B. aurifer* (Hidalgo-García et al. 2018; UNEP-WCMC and IUCN 2021). The Central Plateau has been identified by several authors as a priority region for the conservation of cloud-forest biota in Mexico (Ochoa-Ochoa et al. 2017; Montiel Canales and Goyenechea Mayer 2022). However, both the establishment of new protected areas and the maintenance of existing protected areas require long-term investments, as well as the participation of local communities to ensure that the reserves truly meet biodiversity conservation objectives (Ochoa-Ochoa et al. 2009; Halffter 2011; Méndez-López et al. 2014). The promotion of sustainable non-agricultural livelihoods has also been identified as critical to the success of many reserves in southern Mexico (Auliz-Ortiz et al. 2024). Likewise, we emphasize the need to strengthen the institutions responsible for the conservation of biodiversity and natural resources in Chiapas, by implementing mechanisms for greater surveillance and legality in their activities. Together, these actions are of utmost importance to minimize the loss of habitat for *B. aurifer* and for other imperiled species that inhabit this region.

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

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Author contributions

Conceptualization: JAHG, RLR. Data curation: JAHG. Formal analysis: JAHG. Funding acquisition: JAHG, AGC, JRCV. Investigation: JAHG, RLR, AGC, JRCV. Methodology: JAHG, RLR, AGC. Resources: JAHG, RLR, AGC, JRCV, JGG. Supervision: RLR, AGC. Visualization: JAHG, AGC. Project administration: JAHG, RLR. Software: JAHG. Validation: JAHG, RLR, AGC, JRCV. Writing – original draft: JAHG. Writing – review and editing: JAHG, RLR, AGC, JRCV, JGG, SL.

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Data availability

All data that support the findings of this study are available in the main text. A complete translation into Spanish of the English version of the manuscript is available in the Supplementary Data.

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APPENDIX

Table A1. Localities documented for *Bothriechis aurifer* based on a review of the scientific literature, field records, museum collections, and citizen science platforms. Locality names and their coordinates are intentionally obscured; see Methods for more details and justification.

Country	State or department	Municipality	Locality*	Latitude	Longitude	Elevation (m) [†]	Protected area	Voucher(s) and original source [‡]
Mexico	Chiapas	Yajalón	Vicinity of Lindavista Vesubio/El Delirio	17.18	−092.39	1600	No	LACM PC 3001–3002, 3005, 3010, this study
Mexico	Chiapas	Las Margaritas	Vicinity of Santiago Guelatao	16.49	−091.77	1950	No	UTADC 9407, this study
Mexico	Chiapas	Las Margaritas	Vicinity of Felipe Carrillo Puerto	16.39	−091.73	1660	No	ECO-CH-H-3770, this study
Mexico	Chiapas	La Trinitaria	Lagos de Montebello, between Dos Lagunas and Tziscão [=Parque Nacional Lagunas de Montebello, between Dos Lagunas and Tziscão]	16.09	−091.65	1650	Parque Nacional Lagunas de Montebello	MAT 1148, specimen lost
Guatemala	Alta Verapaz	Carchá	Carchá, Caquipéc, Aldea Chirucbiquim	15.44	−090.19	ca. 1770	No	UTA R-37224, Campbell and Smith 2000
Guatemala	Alta Verapaz	Cobán	Cobán, Verapaz, Guatemala	15.49	−090.35	ca. 1350	No	UTA R-4494, NHMUK 3635686, 3637078
Guatemala	Alta Verapaz	San Cristóbal Verapaz	Baleu	15.38	−090.58	ca. 1410	No	UCM 34300
Guatemala	Alta Verapaz	Santa Cruz Verapaz	Near Cobán	15.33	−090.41	ca. 1450	No	MVZ 201398
Guatemala	Alta Verapaz	Senahú	Finca Volcán	15.47	−089.85	ca. 1410	No	UMMZ 91081
Guatemala	Baja Verapaz	Purulhá	Biotopo Protegido Mario Dary Rivera [=Biotopo “Mario Dary Rivera”]	15.21	−090.22	1520	Biotopo Protegido Mario Dary Rivera	UVG R001489; UTA R-6553, 7716, 8777, Campbell 1982; Arrivillaga et al. 2018
Guatemala	Baja Verapaz	Purulhá	Cerro Quisís	15.19	−090.24	1500–2130	Biotopo Protegido Mario Dary Rivera	KU 187433, 187440, 191196–99, 191200; UTA R-6562, 7039–45, 7763–68, 9608–09, 10434–36, 12552, 22448, Campbell 1982; Campbell and Smith 2000

Country	State or department	Municipality	Locality*	Latitude	Longitude	Elevation (m) [†]	Protected area	Voucher(s) and original source [‡]
Guatemala	Baja Verapaz	Purulhá	Near Unión Barrios, road to Panima	15.21	−090.21	1670	Reserva Natural Privada Ram Tzul	KU 187434, 191203, Campbell 1982
Guatemala	Baja Verapaz	Salamá	Cerro Quisés, near Unión Barrios	15.18	−090.22	1830–2130	No	KU 187430, 187432, 187435–36, Campbell 1982
Guatemala	Baja Verapaz	Salamá	Cerro Quisés, near Unión Barrios	15.17	−090.22	ca. 2130	No	KU 187437, Campbell 1982
Guatemala	Baja Verapaz	Salamá	Cerro Verde	15.18	−090.19	ca. 2260	Reserva Natural Privada Cerro Verde	KU 187427–29, 187431, 187438–39; UTA R-7047, 9366, 12783, 14687, 16064–65, 26574, Campbell 1982; UTA R-1054, Campbell and Smith 2000
Guatemala	Baja Verapaz	Salamá	Cumbre del Carpintero	15.15	−090.17	ca. 1660	No	UVG R001093
Guatemala	Baja Verapaz	Salamá	La Unión Barrios	15.17	−090.21	1530	No	UTA R-6241, 6275–76, 6459, 6504–05, 6525, 6553, 7046, 7048, 7635–36, 7762, 7788, 12949–51, 13030–31, 13614–16, 14213, 14223, 16060–63, 17906, 21842, 22439–47, 22449, 26163–64, 26388–91, 31207, 31978, 32085–86, 32424, 34486, 35031, 36211, 46660–61, 51727–28, 54306–07, Campbell 1982; Campbell and Smith 2000; UVG R002245, 000140; ROM 42220–21
Guatemala	Baja Verapaz	Salamá	Niño Perdido	15.15	−090.11	ca. 1860	Reserva de la Biósfera Sierra de las Minas	UTA R-39219–23, 45870–1, 28551–52, Campbell and Smith 2000
Guatemala	Baja Verapaz	Salamá	Near La Unión Barrios	15.18	−090.17	1590–1710	Reserva Natural Privada Cerro Verde	KU 191202, Campbell 1982; UTA R-46659,
Guatemala	El Quiché	San Juan Cotzal	Near Palo Viejo hydroelectric dam on road to La Gloria	15.51	−090.86	1500	No	MVZ 265626
Guatemala	El Quiché	Chicamán	Near Cobán, Finca El Soche	15.47	−090.75	ca. 2140	No	CAS 67049, Campbell 1982
Guatemala	Huehuetenango	Nentón	Aldea Yalamboloh, Finca San Francisco	15.97	−091.56	ca. 1970	No	UTA R-46668, 46893–94; Mendelson et al. 2012
Guatemala	Huehuetenango	Santa Cruz Barillas	Santa Cruz Barillas	15.95	−091.31	1430	No	iNaturalist #38889522
Guatemala	Zacapa	Teculután	Near San Lorenzo	15.18	−089.66	ca. 1210	Reserva de la Biósfera Sierra de las Minas	KU 191201, Campbell 1982

*Square brackets “[]” indicate an alternative or more precise locality description.
[†]All elevation data are rounded to the nearest 10 m, and elevation values preceded by “ca.” are rough estimates due to the imprecision of the locality data.
[‡] California Academy of Sciences, San Francisco (CAS); El Colegio de la Frontera Sur, Chetumal (ECO-CH-H); Colección Zoológica Regional Herpetológica, Secretaría de Medio Ambiente e Historia Natural, Tuxtla Gutiérrez (CZR-HE); University of Kansas Biodiversity Institute, Lawrence (KU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Natural History Museum, London (NHMUK); Royal Ontario Museum, Toronto (ROM); University of Colorado Museum of Natural History, Boulder (UCM); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); University of Texas at Arlington (UTA); University of Texas at Arlington–Digital Collection (UTADC); Universidad del Valle de Guatemala, Guatemala City (UVG).